

Biological relevance of polyploidy: ecology to genomics

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Polyploidy in arctic plants

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The Arctic is an excellent model system for the study of polyploidy. It is one of the Earth's most polyploid-rich areas, in particular of high-level and recently evolved polyploids. Here we re-address previous hypotheses on arctic polyploidy based on a new analysis of the circumarctic flora, and review recent molecular, cytological and reproductive studies. The frequency and level of polyploidy strongly increase northwards within the Arctic. We found no clear-cut association between polyploidy and the degree of glaciation for the arctic flora as a whole, which contains many wide-spread species. However, for 'arctic specialist' taxa with restricted distributions, the frequency of diploids is much higher in the Beringian area, which remained largely unglaciated during the last ice age, than in the heavily glaciated Atlantic area. This result supports the hypothesis that polyploids are more successful than diploids in colonizing after deglaciation. There is abundant molecular evidence for recurrent formation of arctic polyploids at different scales in time and space. Examples are given of low-level polyploids formed after the last glaciation and of repeated and successively more high-level polyploidizations throughout the Quaternary. Recurrent polyploid origins, followed by interbreeding within and across ploidal levels, provide a major explanation for the taxonomic complexity of the arctic flora. In the well-studied, recently deglaciated archipelago of Svalbard, most species are mainly self-fertilizing or clonal. All Svalbard polyploids examined so far are genetic allopolyploids with fixed heterozygosity at isozyme loci. The level of heterozygosity in 65 taxa increases dramatically from diploids to high-level polyploids. In the circumarctic area, there is evidence for numerous recently evolved sibling species within diploid taxonomic species. Rapid evolution of crossing barriers at the diploid level promotes further diversification after expansion from different refugia, and may provide new raw materials for allopolyploid formation. We conclude that the evolutionary success of polyploids in the Arctic may be based on their fixed-heterozygous genomes, which buffer against inbreeding and genetic drift through periods of dramatic climate change. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **82**, 521–536.

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INTRODUCTION

The Arctic flora has been shaped through numerous large-scale climate changes resulting in cycles of fragmentation, range expansion and reunion of previously isolated populations (Stebbins, 1984, 1985). The early

Quaternary flora was probably recruited from survivors of the arcto-Tertiary forests combined with immigrants from temperate mountain ranges (Murray, 1995). This floristic mixture has since repeatedly been spatially re-arranged and re-mixed, and today, the majority of arctic plants appear to be of hybrid origin, many of them between plants which themselves are, or were, of hybrid origin. Most of these hybrids have been stabilized via polyploidy. Successive cycles of

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divergent evolution among populations isolated in different glacial refugia, migration into deglaciated terrain, hybridization and polyploidy have built up increasingly intricate, high-ploid mixtures (Abbott & Brochmann, 2003).

The last 2–3 million years have transformed the Arctic into an excellent model system for the study of polyploidy. Today, it is one of the most polyploid-rich areas, with numerous and very high polyploids. The tundra abounds with recent polyploids, formed at various scales in time and space during the Quaternary, some of them during the 10 000 years since the last major deglaciation. Thus, the Arctic provides many ideal study groups for addressing the effects of recent gene duplications and their expressions, the mode and frequency of formation of polyploids, and the evolutionary significance of polyploidy.

It has been known for a long time that the frequency of polyploidy increases with latitude in the northern hemisphere. The possible reasons for this trend have been discussed for many decades. Hagerup (1931) proposed that polyploids are better adapted than diploids to extreme climates. Manton (1950), Löve & Löve (1957), Johnson & Packer (1965) and Johnson, Packer & Reese (1965) believed that polyploids are at selective advantage where climatic fluctuations have been frequent and catastrophic, because they have great genetic variability resulting from recent hybridization. Stebbins (1950) argued that polyploids seem to be better suited than diploids to colonize newly deglaciated areas because of greater ecological adaptability.

The lively discussions from the 1930s to the 1970s were summarized by Stebbins (1984, 1985). He refuted the classical 'increased hardiness hypothesis', i.e. that polyploids have greater resistance than diploids to the harsh arctic climate. By comparing different floras along the Pacific coast of North America, Stebbins (1984) found higher frequencies of polyploids at 52–54°N (a previously glaciated area) than at 63–71°N (northern Alaska; largely unglaciated), where the frequencies were no higher than in Central Europe. His observation led him to suggest that there is a correlation between polyploid frequencies and degree of glaciation, rather than with latitude *per se*. He also found that the frequencies were higher at the same latitude in insular regions than on continents.

Stebbins' (1984) 'secondary contact hypothesis' is an extension of his former view that polyploidy serves to stabilize favourable new gene combinations derived from hybridization between races that have different adaptive norms. In the Arctic, secondary contacts between populations, which have diverged in different refugia, are repeatedly established and broken. Hybridization and polyploidy generate new races and species, some of which become adapted to the new conditions in regions vacated by ice. Stebbins (1985)

found further evidence to strengthen his view that success of polyploids is a result of increased heterozygosity accompanying hybridization.

In the proceedings from the previous international conference on polyploidy (Lewis, 1980), Stebbins (1980) summarized unresolved problems and prospects for future research on polyploidy. Some of these problems were followed up in his 1984 and 1985 reviews discussed above (see also Stebbins & Dawe, 1987, for a general discussion on polyploidy and distribution). In Ehrendorfer's (1980) contribution to this conference, he concluded that there are no direct and general causal connections between polyploidy on the one hand and ecology, habitat or distribution on the other. However, he did find that successful neopolyploids tend to originate under unstable conditions, in areas of contact and hybridization, and in invasive and successional floras, although he did not address arctic floras in particular. Ehrendorfer (1980) concluded by calling for more comprehensive analyses of polyploid complexes and karyological surveys of diverse floras.

In this paper, we re-address some of the hypotheses and generalizations discussed above by examining new evidence accumulated for the arctic flora (see Levin, 2002, for a general review of chromosomal evolution). We provide a new analysis of the frequency and levels of polyploidy in the entire arctic flora, made possible by the completion of the draft version of the critical *PanArctic Flora Checklist* (Elven *et al.*, 2003). We have put particular emphasis on the levels of ploidy, as advocated by Löve & Löve (1957); most previous analyses have only addressed the frequency of polyploids. Based on the entire arctic flora, we re-examine Stebbins' (1984) observations based on local American floras that the frequency of polyploidy is correlated with degree of glaciation rather than with latitude *per se*.

We further review recent case studies based on molecular and biogeographical analyses of arctic polyploids, with particular reference to recurrent formation (see Soltis & Soltis, 1993, 1999, 2000, for general reviews; Abbott & Lowe, 2004, and Soltis *et al.*, 2004 – both this issue, for reviews of recent recurring origins in *Senecio* and *Tragopogon*, respectively; and Ainouche, Baumel & Salmon, 2004 – also this issue, for an example of recent single-origin polyploidy in *Spartina*). Genetic, reproductive and ecological consequences of arctic polyploidy are addressed with particular reference to the recently deglaciated North Atlantic archipelago of Svalbard, where many molecular and reproductive studies have been conducted during the last two decades. In an analysis of the Svalbard flora, we provide new quantitative estimates of the levels of heterozygosity based on 40% of the species, with particular reference to the hypothesis that

the success of polyploids is associated with increased heterozygosity. We finally review recent reports suggesting that sibling (cryptic) species can be common within arctic diploid taxonomic species and relate these findings to observations of variable levels of heterozygosity among arctic allopolyploids.

FREQUENCY, LEVEL AND DISTRIBUTION OF ARCTIC POLYPLOIDY

DATA COLLECTION AND HYPOTHESES

The recent completion of the draft version of the critical *PanArctic Flora* (PAF) *Checklist* (Elven *et al.*, 2003) has made it possible for the first time to make a full circumpolar analysis of arctic polyploidy. The PAF project is based on a collaboration between most arctic countries (Norway, Iceland, Russia, Canada, USA) and headed by R. Elven and I. Nordal, Oslo (see Nordal & Razzhivin, 1999). The completion of a checklist for this vast geographical area is a major achievement because the taxonomic traditions differ considerably among Europe, the former USSR and North America. In addition, numerous discrepancies had to be resolved because of inherent problems with the arctic flora *per se*; there are notorious taxonomic complexities because of reticulate evolution, inbreeding/asexuality and occurrence of very widespread taxa.

The PAF checklist accepts 2164 taxa at the species and subspecies level within the Arctic as delimited in Elvebakk, Elven & Razzhivin (1999). All original chromosome number reports are included, for which many of the vouchers have been re-examined. Chromosome numbers are available for the vast majority of taxa (91%; 1971 taxa). For the present analysis, we further excluded 81 introduced taxa, 159 taxa of the Cyperaceae (mainly *Carex*; basic chromosome numbers difficult to infer because of diffuse centromeres causing frequent chromosome fission) and 12 taxa of *Alchemilla* (basic chromosome number difficult to estimate). The final data matrix thus contained 1719 taxa or 79% of the total arctic flora (83% of the indigenous arctic flora). Basic chromosome numbers and ploidy were inferred based on the lowest chromosome number known in each genus or infrageneric group, or in some cases, based on ploidal levels inferred from number of duplications visible on isozyme gels (see Brochmann & Steen, 1999, and references therein). For nearly 10% of the taxa analysed, both diploid and polyploid chromosome numbers have been reported (classified as 'diploids/polyploids' in Table 2). Several ploidal levels have been reported also within many polyploid taxa, for which the mean value was used in the calculations (e.g. $7x$ if both $6x$ and $8x$ have been reported).

The PAF checklist (Elven *et al.*, 2003) divides the

Arctic into five zones reflecting the south–north gradient, ranging from the southernmost border areas towards the Boreal (zone 1) to the Polar Desert (zone 5; see also Elvebakk, 1999; Elvebakk *et al.*, 1999). Herein we classify the arctic taxa into five 'zonal groups' based on these zones, ranging from mainly boreal or temperate alpine taxa that only have a few borderline occurrences in the Arctic (zonal group 1) to extreme arctic specialists that exclusively occur in the Arctic (zonal group 5; see Table 1 for full definitions). We further designated the taxa of zonal groups 2–5 as 'regularly arctic taxa' (1030 taxa) and those of zonal groups 4–5 as 'arctic specialist taxa' (228 taxa; Table 2). In addition, the checklist gives the distribution of each taxon according to a sectorial subdivision of the Arctic, roughly reflecting a longitudinal gradient with different degrees of ice cover during the last glaciation (Elvebakk *et al.*, 1999; Table 2). For our analysis, we also addressed the association between polyploidy and glaciation by classifying taxa into an 'Atlantic group', comprising all taxa with their main occurrence restricted to the formerly glaciated part of the Atlantic area, and a 'Beringian group', comprising all taxa with their main occurrence restricted to the Beringian area, which remained largely unglaciated during the last glaciation (cf. Fig. 2). We used these data to test the hypotheses that not only the frequency of polyploidy, but also the level of polyploidy, increases northwards within the Arctic, and that the frequency and level of polyploidy are highest in previously glaciated areas of the Arctic.

POLYPLOIDY ALONG THE ARCTIC SOUTH–NORTH GRADIENT

The total arctic flora contains many diploid species (~50%; including taxa with both diploid and polyploid populations), but many of these have their main occurrence in boreal and/or temperate alpine areas (zonal groups 1 and 2; Tables 1, 2). By contrast, among the arctic specialist taxa (zonal groups 4 and 5), the vast majority are exclusively polyploid (73.7%).

The frequency of diploids strongly and regularly decreases along the S–N zonal gradient (from 46.0% to 16.7%; Table 1, Fig. 1). Correspondingly, the frequency of exclusively polyploid taxa increases from 43.8% to 82.1%. However, the frequencies along this gradient differ markedly between polyploid levels. Whereas the frequency of the lower polyploids is roughly constant, the frequency of the higher polyploids increases dramatically (e.g. $\geq 9x$: 2.7–17.8%). For all polyploids above the tetraploid level, the frequency increases from 19.0% to 55.9% (Fig. 1). The mean ploidal level for the arctic borderline taxa (zonal group 1) is less than tetraploid (3.6), whereas the mean for the extreme arctic specialist taxa (zonal group 5) is hexa-

Table 1. Frequency and level of polyploidy in the arctic flora along the south–north gradient, based on 1719 taxa classified according to the south–north zonal subdivision of the Arctic in Elvebakk *et al.* (1999). Zonal group 1 – boreal and/or temperate alpine taxa with few arctic occurrences; zonal group 2 – boreal and/or temperate alpine taxa with frequent to common occurrences in one arctic zone; zonal group 3 – boreal and/or temperate alpine taxa with frequent to common occurrences in two or more arctic zones; zonal group 4 – mainly arctic taxa with infrequent occurrences in boreal and/or temperate alpine areas; zonal group 5 – exclusively arctic (or nearly so) taxa. The taxa in zonal groups 2–5 are defined as ‘regularly arctic taxa’, and the taxa in zonal groups 4 and 5 are defined as ‘arctic specialist taxa’. Taxa including diploid as well as polyploid populations are designated ‘diploid/polyploid’. Taxa with several reported ploidal levels are placed in ploidal level group (3–4x, 5–6x, etc.) based on their mean ploidal level. *N*, number of taxa

Ploidal level(s)	Zonal group									
	1		2		3		4		5	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
Diploids	317	46.0	173	42.1	134	34.3	39	27.1	14	16.7
Diploids/polyploids	70	10.2	41	10.0	47	12.0	6	4.1	1	1.2
Polyploids	302	43.8	197	47.9	210	53.7	99	68.8	69	82.1
3–4x	241	35.0	136	33.1	127	32.5	50	34.7	23	27.4
5–6x	77	11.2	57	13.9	57	14.5	20	13.9	14	16.7
7–8x	35	5.1	27	6.6	32	8.2	16	11.1	18	21.4
≥9x	19	2.7	19	4.6	41	10.5	19	13.2	15	17.8
Total no. of taxa	689		411		391		144		84	
Mean ploidal level	3.6		3.9		4.4		5.0		6.0	

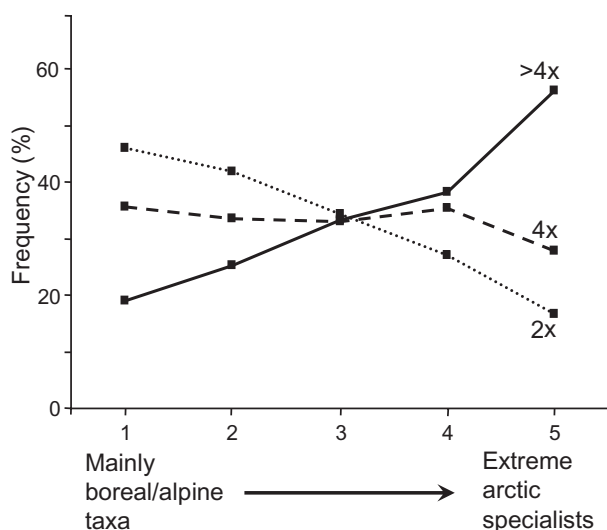


Figure 1. Frequency and level of polyploidy in the arctic flora along the south–north gradient, based on 1719 of the chromosome-counted taxa in the Panarctic Flora checklist (excluding most Cyperaceae etc., see text). The taxa are classified into zonal groups according to the south–north zonal subdivision of the Arctic in Elvebakk *et al.* (1999). See Table 1 for definition of zonal groups.

ploid (6.0; Table 1). Thus, our new data corroborate earlier observations that the frequency of polyploids increases with latitude, even within the Arctic, and we have shown that this general increase is caused by increasing frequencies of high polyploids (above the tetraploid level).

POLYPLOIDY AND GLACIATION

The analysis based on sections (the east–west gradient) gave only vague trends (Table 2). The mainly non-glaciated sections (the Beringian and Siberian sections) tend to harbour somewhat more diploids and somewhat fewer high polyploids than the mainly glaciated sections (the Atlantic sections), but this trend is weak even for the arctic specialist taxa. Notably, this analysis included all taxa, many of which occur in several sections or have a complete circumpolar distribution.

By contrast, the analysis based on taxa restricted to the main glaciated region (Atlantic) or to the main non-glaciated region (Beringia) resulted in a distinct pattern. Among the arctic specialist taxa with such restricted distributions, the proportion of diploids is much higher in Beringia (25.9%) than in the Atlantic area (10.5%; Table 2, Fig. 2). The frequency of exclu-

Table 2. Frequency and level of polyploidy in the arctic flora with reference to main areas of glaciation, a longitudinal gradient (sectorial subdivision) and a south–north gradient (zonal subdivision), based on 1719 taxa. Glaciated/non-glaciated area: Atlantic group – taxa with their main occurrence restricted to the glaciated part of the Atlantic area; Beringian group – taxa with their main occurrence restricted to the non-glaciated parts of the Beringian/Pacific area (cf. Fig. 2). East–west gradient (sections): Europe Atl – Atlantic parts of Europe; Europe Cont – Continental Europe; Siberia NW – NW continental Siberia; Siberia NE – NE continental Siberia; Beringia W – Western (Asiatic) Beringia and Pacific coast; Beringia E – Eastern (American) Beringia and Pacific coast; Amer Cont – Continental North America; Amer Atl – Atlantic North America, incl. Greenland. South–north gradient (zonal groups): See Table 1 for explanation. The subdivision of the Arctic follows Elvebakk *et al.* (1999). *N*, number of taxa

		Diploids 2x		Diploids/ polyploids		Polyploids >2x		Low polyploids 3–4x		High polyploids >4x		Mean ploidal level
	Total	N	%	N	%	N	%	N	%	N	%	
All taxa (zonal groups 1–5)												
Total	1719	676	39.3	165	9.6	878	51.1	577	33.6	466	27.1	4.1
Glaciated/non-glaciated area												
Atlantic	155	43	27.8	7	4.5	105	67.7	52	33.5	60	38.7	5.1
Beringian	370	128	34.6	41	11.1	201	54.3	118	31.9	124	33.5	4.4
Sections												
Europe Atl	611	222	36.3	40	6.5	349	57.2	213	34.9	176	28.8	4.2
Europe Cont	619	240	38.8	59	9.5	320	51.7	208	33.6	171	27.6	4.1
Siberia NW	588	217	36.9	67	11.4	304	51.7	198	33.7	173	29.4	4.2
Siberia NE	560	212	37.9	64	11.4	284	50.7	180	32.1	168	30.0	4.2
Beringia W	763	286	37.5	76	10.0	400	52.5	245	32.1	232	30.4	4.2
Beringia E	795	306	38.5	85	10.7	404	50.8	271	34.1	218	27.4	4.1
Amer Cont	774	306	39.5	69	8.9	399	51.6	255	33.0	213	27.5	4.0
Amer Atl	440	149	33.8	24	5.5	267	60.7	142	32.3	149	33.9	4.6
Regularly arctic taxa (zonal groups 2–5)												
Total	1030	359	34.9	95	9.2	576	55.9	336	32.6	335	32.5	5.3
Glaciated/non-glaciated area												
Atlantic	129	34	26.4	5	3.9	90	69.7	39	30.2	56	43.4	5.3
Beringian	312	104	33.3	37	11.9	171	54.8	97	31.1	111	35.6	4.5
Sections												
Europe Atl	443	155	35.0	26	5.9	262	59.1	147	33.2	141	31.8	4.5
Europe Cont	484	174	35.9	44	9.1	266	55.0	165	34.1	145	30.0	4.3
Siberia NW	485	171	35.3	54	11.1	260	53.6	161	33.2	153	31.5	4.3
Siberia NE	464	166	35.8	55	11.8	243	52.4	149	32.1	149	32.1	4.4
Beringia W	631	221	35.0	67	10.6	343	54.4	205	32.5	205	32.5	4.4
Beringia E	587	212	36.1	63	10.7	312	53.2	192	32.7	183	31.2	4.3
Amer Cont	506	177	35.0	42	8.3	287	56.7	163	32.2	166	32.8	4.4
Amer Atl	389	128	32.9	22	5.7	239	61.4	120	30.9	141	36.2	4.7
Arctic specialist taxa (zonal groups 4–5)												
Total	228	53	23.2	7	3.1	168	73.7	73	32.0	102	44.8	5.4
Glaciated/non-glaciated area												
Atlantic	38	4	10.5	1	2.6	33	86.9	10	26.3	24	63.2	6.6
Beringian	85	22	25.9	4	4.7	59	69.4	22	25.9	41	48.2	5.4
Sections												
Europe Atl	94	19	20.2	2	2.1	73	77.7	35	37.2	40	42.6	5.2
Europe Cont	95	21	22.1	4	4.2	70	73.7	39	41.1	35	36.8	4.9
Siberia NW	100	22	22.0	5	5.0	73	73.0	39	39.0	39	39.0	4.9
Siberia NE	104	23	22.1	5	4.8	76	73.1	38	36.5	43	41.4	5.1
Beringia W	161	36	22.4	6	3.7	119	73.9	52	32.3	73	45.3	5.1
Beringia E	121	30	24.8	6	5.0	85	70.2	41	33.9	50	41.3	5.0
Amer Cont	123	29	23.6	3	2.4	91	74.0	39	31.7	55	44.7	5.4
Amer Atl	114	22	19.3	3	2.6	89	78.1	35	30.7	57	50.0	5.6

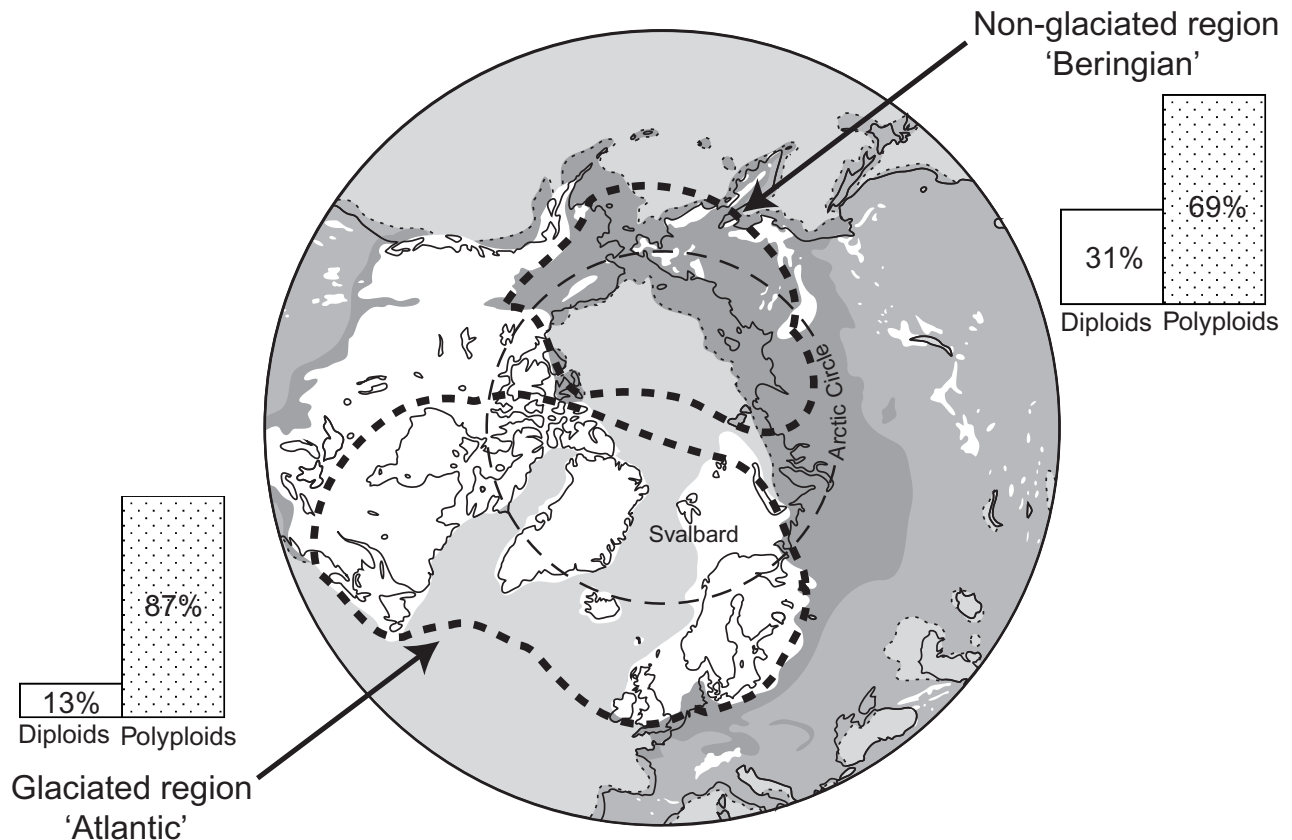


Figure 2. Frequency of polyploidy among 'arctic specialist taxa' (zonal groups 4 and 5; cf. Tables 1, 2) that are either restricted to the region that was heavily glaciated during the last ice age ('Atlantic') or restricted to the region that remained mainly unglaciated ('Beringian'). The maximum extent of the late Weichselian/Wisconsinian ice sheets (white) and tundra (dark grey) are shown, modified after Abbott & Brochmann (2003) and Brochmann *et al.* (2003).

sively polyploid taxa restricted to the Atlantic area is extremely high (86.9%). Whereas the frequencies of low polyploids are similar for the two regions, the Atlantic region harbours more high-level polyploids than Beringia (63.2% vs. 48.2%). Similar but much less distinct patterns were observed for the total arctic flora and for the regularly arctic taxa (Table 2).

We also analysed the proportions of diploid vs. polyploid members of some large genera along the sectorial gradient. We observed no clear patterns except in the grass genus *Puccinellia*. This genus has 30 currently accepted arctic species and subspecies. Whereas there are similar numbers of diploid and polyploid taxa in the two Beringian sectors (six vs. six and six vs. seven in W and E Beringia, respectively), there are few diploid and many polyploid taxa in the Atlantic sectors (two vs. 11 and one vs. eight in the American and European Atlantic, respectively). The continental sectors in America and Europe are intermediate (five vs. nine and two vs. four, respectively), whereas the Siberian sectors resemble the Atlantic sector (one vs.

five in NW and one vs. seven in NE, respectively). This pattern may suggest that Beringian diploid stocks have formed polyploids that migrated eastwards and westwards into deglaciated areas.

We conclude that when analysing the arctic flora as a whole, there is no strong or clear-cut general association between frequencies or levels of polyploidy and degree of glaciation, as found by Stebbins (1984) in his analysis of North American regional floras. It is possible that local patterns have been confounded by the very widespread occurrence of many high arctic polyploids as well as diploids. However, when only the arctic specialist taxa that are restricted to the mainly glaciated Atlantic area or to the mainly non-glaciated Beringian area are considered, there is a much lower frequency of diploids in the Atlantic area. This pattern may suggest that after the last deglaciation, when many taxa now exclusively occurring in the Atlantic Arctic were recruited from nearby regions, polyploids were more successful than diploids in colonizing deglaciated areas. In the major arctic refugium of Ber-

ingia, on the other hand, both diploids and polyploids probably survived *in situ* during several glaciations.

RECURRENT POLYPLOIDY AND RECONSTRUCTION OF RETICULATIONS

Reconstruction of the evolutionary histories of arctic plants is not an easy task. The high frequency and level of polyploidy, the predominance of autogamous and asexual reproductive systems, and the repeated large-scale spatial reshuffling of populations during the glacial cycles complicate any inference on biogeographical and phylogenetic relationships. In addition, there is now increasing evidence for widespread recurrent formation of similar arctic polyploids from more or less divergent diploid/low-polyploid progenitors. The intriguing taxonomic complexity of the arctic flora can probably be explained to a large degree by recurrent hybridization and polyploidization, and subsequent interbreeding of the resulting genotypes.

We review below some recent case studies addressing the origins of polyploids, with particular reference to recurrent polyploid formation. Polyploidization has probably occurred repeatedly throughout the entire Quaternary, resulting in intricate and very high-ploid complexes in many plant groups. Therefore, we will first review two simple cases of recent, probably post-Weichselian tetraploidizations. These species are not really arctic, but they provide excellent illustrations of polyploidization events that can be directly associated with recent deglaciation.

RECENT DEGLACIATION AND ALLOTETRAPLOIDY: *SAXIFRAGA OSLOENSIS*

A very simple example of polyploid speciation that probably took place in connection with the retreat of the Weichselian glacier is represented by the allotetraploid Scandinavian endemic *Saxifraga osloensis* Knaben (Knaben, 1954; Brochmann, Nilsson & Gabrielsen, 1996; Nilsson & Jorde, 1998). This species is narrowly distributed in a zone between the currently alpine Scandinavian distribution of the diploid *S. adscendens* L. and the lowland distribution of the diploid *S. tridactylites* L. Whereas the cpDNA of *S. osloensis* is identical to that of *S. adscendens*, but very divergent from that of *S. tridactylites*, its nuclear multilocus genotypes at RAPD and isozyme loci can be obtained by adding markers observed in these two diploid species. Interestingly, the annual *S. osloensis* is virtually identical to *S. adscendens* also in ITS, suggesting that sufficient time has elapsed for rDNA homogenization in the direction of its presumably maternal progenitor. *Saxifraga osloensis* is genetically allopolyploid, as shown by its fixed heterozygosity at isozyme loci. Thus, the fully sexual and autogamous

allotetraploid *S. osloensis* has most likely originated *in situ* by hybridization between these two diploid species after the last glaciation. The alpine diploid *S. adscendens* probably immigrated first, after the retreating ice, followed by the more thermophilous diploid *S. tridactylites*. So far, too few populations have been analysed to address the possibility for multiple origins of *S. osloensis*.

RECENT DEGLACIATION AND RECURRENT AUTOTETRAPLOIDY: *PARNASSIA PALUSTRIS*

The circumpolar, outcrossing species *Parnassia palustris* L. s. l. consists of several cytotypes, of which diploids and tetraploids are dominating. The species has been extensively investigated in Europe, in particular in Scandinavia, based on allozyme electrophoresis and ploidy determinations (Hultgård, 1987; Borgen & Hultgård, 2003). The diploids are mainly found in the central and southern European mountains, but extend northwards to southern Scandinavia, and the tetraploids are mainly found in northern Europe. A distinct zone of overlap is found across southern Scandinavia, corresponding to the glacial boundary 10 000 years ago (a similar zone of overlap occurs in the British Isles; Gornall & Wentworth, 1993). The tetraploid populations are highly heterozygous and possess the same alleles as diploid *P. palustris* in various balanced and unbalanced combinations. Thus, they are probably autotetraploids with tetrasomic inheritance. Borgen & Hultgård (2003) also found strong evidence for recurrent formation of the tetraploids, based on parallel variation at isozyme loci among different diploid and tetraploid populations. This result is in accordance with observations of parallel variation in morphological characters, suggesting that the previously recognized subspecies based on ploidal level and geographical distribution cannot be retained. At least some of the tetraploid populations probably originated in southern Scandinavia after the last glaciation and were evidently more successful than the diploids in colonizing new land following the retreat of the ice.

RECURRENT FORMATION OF TETRAPLOIDS AT DIFFERENT TIME SCALES: *VACCINIUM ULIGINOSUM*

A more complex example of recurring tetraploidy, involving events that probably have taken place at different scales in time and space, is represented by the bird-dispersed arctic blueberry (or bilberry), *Vaccinium uliginosum* L. s. l. These insect-pollinated dwarf shrubs are key components of several northern ecosystems, ranging from boreal forests and bogs to alpine heaths and arctic tundra. The complex has a complete circumpolar/boreal distribution with extension to more southern mountain ranges. About 30 different

taxa have been described in this complex, some of them at the species level, but a single, polymorphic species with a variable number of subspecies is now usually recognized.

Recent molecular, ploidal and morphological analyses of populations from the entire distribution range have provided strong evidence for at least three and

probably more independent origins of tetraploids (Alsos *et al.*, 2001; Alsos, Engelskjøn & Brochmann, 2002; Alsos, 2003; I. G. Alsos, T. Engelskjøn, J. Suda, L. Gielly, P. Taberlet & C. Brochmann, unpubl. data). Three major clades were identified in phylogenetic analyses of non-coding cpDNA (Fig. 3): the circumpolar 'Arctic-Alpine Clade', the boreal 'Amphi-Atlantic

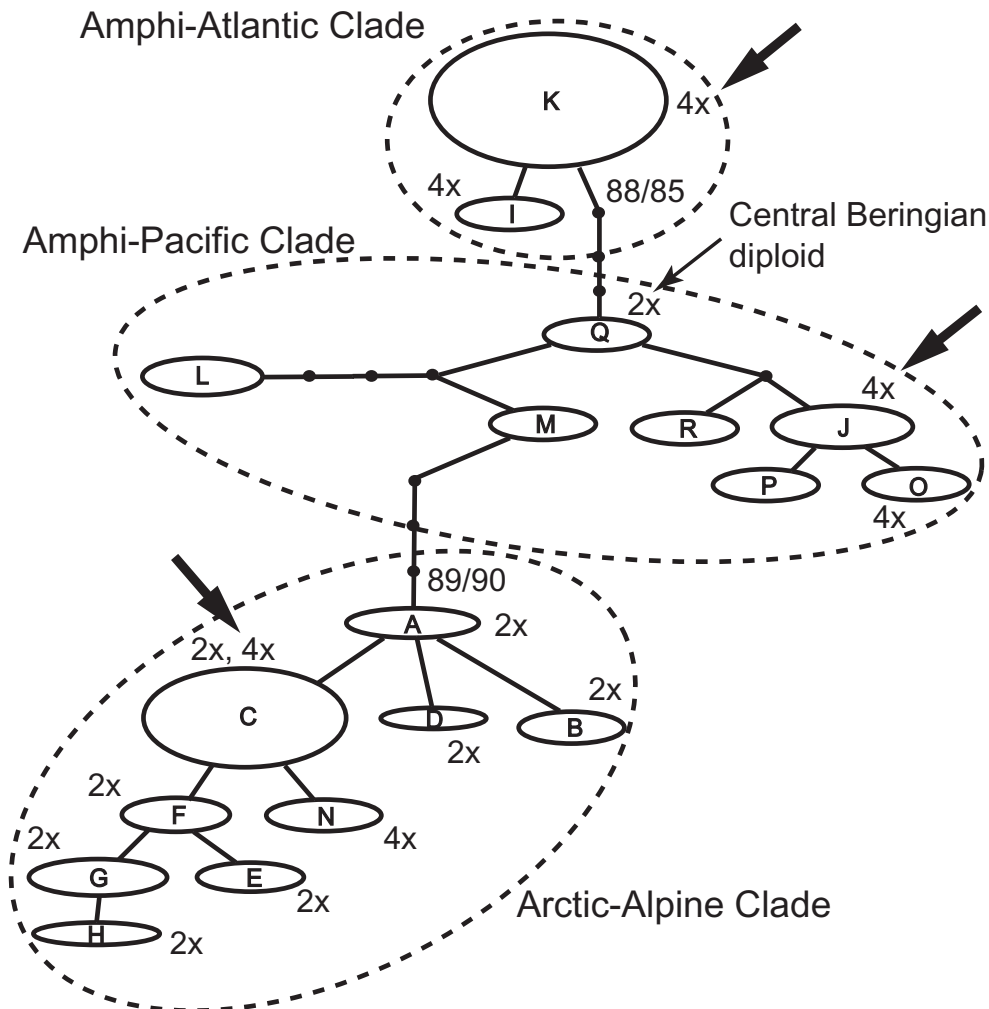


Figure 3. Multiple origins of tetraploids (thick arrows) at different scales in time and space in the arctic blueberry (bilberry) complex, *Vaccinium uliginosum* coll. A central Beringian diploid is indicated with a thin arrow. Ploidal levels inferred from chromosome counts and flow cytometry are superimposed on the estimated 95% plausible set of haplotype networks for the 18 combined chloroplast DNA haplotypes (designated by letters; based on *trnL/F* and *trnS/G* spacer region sequences) observed in a circumpolar analysis of 122 populations. Lines indicate the mutational pathway interconnecting the 18 haplotypes; dots indicate inferred intermediate haplotypes not observed in the samples. Size of ovals reflects sample size. The three major clades identified in phylogenetic analyses of the cpDNA haplotypes are circumscribed by dotted lines. The relationships among these clades were unresolved, but two of them had high bootstrap support in maximum parsimony/maximum likelihood analyses (support values are indicated on the haplotype network). The bootstrap support for the Amphi-Pacific (Beringian) Clade, which occupies the central position in the network, was moderate (66/75). The three clades were estimated to have diverged between 3.0 and 0.7 Mya, and the origin of tetraploidy in the widespread and exclusively tetraploid Amphi-Atlantic Boreal Clade may date to this period. Tetraploidy has probably originated recurrently and more recently in the other clades. Based on I. G. Alsos, T. Engelskjøn, J. Suda, L. Gielly, P. Taberlet & C. Brochmann, unpubl. data (see Alsos, 2003).

Clade' and the boreal/Beringian 'Amphi-Pacific Clade', estimated to have diverged between 0.7 and 3.0 Mya. The Amphi-Pacific Clade was diverse and formed a central group in a network analysis, with the chloroplast haplotype of a Beringian diploid in the most central position, suggesting that the entire complex may have originated in Beringia (Fig. 3). The Amphi-Atlantic Clade was exclusively tetraploid, suggesting that this lineage was derived from an old tetraploidization event, possibly dating back to the onset of the Pleistocene glaciations. By contrast, the tetraploids in the Amphi-Pacific Clade were confined to tip haplotypes in the network analysis, which may suggest more recent origins. In the Arctic-Alpine Clade, most populations were diploid, but the most widespread (entirely circumpolar) haplotype C was also found in tetraploid populations, suggesting that tetraploidy has originated independently and more recently also in this clade.

RECURRENT FORMATION OF HIGHER POLYPOIDS AT THE CIRCUMARCTIC SCALE: *DUPONTIA*

Dupontia (Poaceae) is exclusively arctic and quantitatively important in wetland vegetation. It is predominantly asexual and shows several high ploidal levels in the circumarctic area. The genus probably arose via hybridization and polyploidization, possibly involving members of the genera *Arctophila* and *Poa*. Several recent studies have addressed taxonomic relationships and polyploid evolution in *Dupontia*, based on cpDNA sequencing, sequencing of cloned copies of nrDNA, AFLP-fingerprinting, fluorescence *in situ* hybridization (FISH), chromosome number determination, flow cytometry and morphological analysis (Brysting *et al.*, 2003; Brysting *et al.*, 2004). Several species have been described within the genus, partly based on differences in ploidy, but new data suggest that the genus should be considered monotypic with only a single, morphologically variable species (*D. fisheri* R. Br.; Brysting *et al.*, 2003, 2004, and unpubl. data).

Dupontia only consists of polyploids. The most common chromosome numbers are $2n = 42-44, 84-88$ and $126-132$. These numbers represent hexaploids ($6x$), dodecaploids ($12x$) and 18-ploids, respectively, if we assume a basic number of $x = 7$ as in most members of the core Pooideae (Grass Phylogeny Working Group, 2001). The variation observed at each ploidal level can either be caused by aneuploidy or by variable presence of B chromosomes. The higher polyploids have probably arisen within the genus itself. Although all plants are fixed-heterozygous at isozyme loci, suggesting genetic allopolyploidy, the high degree of similarity observed between the isozyme and AFLP profiles of lower and higher polyploids suggests that the low-

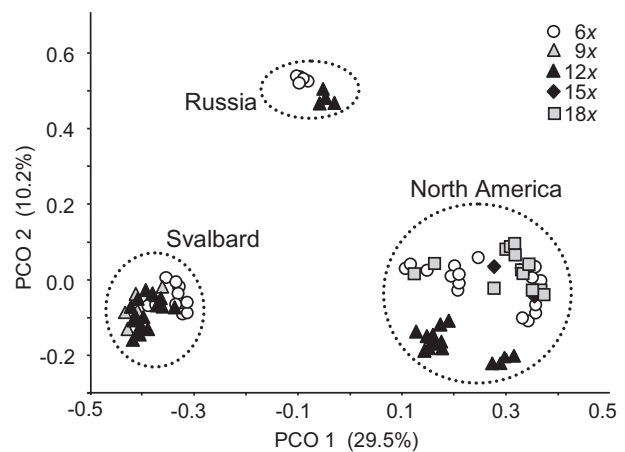


Figure 4. Recurrent formation of high polyploids at the circumarctic scale in the arctic grass genus *Dupontia*. Ploidal levels estimated by chromosome counting and flow cytometry are superimposed on a principal coordinate analysis based on AFLP fingerprint data. The grouping of populations according to geographical origin rather than ploidal level was also observed in parsimony analysis, where the three geographical groups obtained high bootstrap support. The pattern suggests that after initial colonization of the circumarctic area by hexaploids ($6x$), dodecaploids ($12x$) originated at least three times. Modified from Brysting *et al.* (2004; cf. also Brysting *et al.*, 2003).

polyploid progenitors of the high polyploids were very closely related.

The AFLP and ploidy data provide compelling evidence for independent formation of higher polyploids in different geographical areas. In parsimony, UPGMA and PCO analyses of the AFLP data, three distinct groups corresponding to North America, Russia and Svalbard were identified, each including plants of several ploidal levels (Fig. 4). This pattern suggests that the circumarctic area initially was colonized by hexaploids, which subsequently gave rise to higher polyploids in different areas. The dodecaploids have, for example, originated at least three times (Fig. 4).

RAPID HIGH POLYPOIDIZATIONS AND CIRCUMARCTIC COLONIZATION: *CERASTIUM*

Far more complex histories of reticulations are found in *Cerastium*, a large and taxonomically intricate genus with many high-polyploid species. Recent molecular and morphological studies of the dodecaploid ($2n = 12x = 108$), amphi-Atlantic *C. arcticum* Lange s. l. revealed that it consists of two highly divergent dodecaploid lineages, which probably have different polyploid origins and now are recognized as two distinct taxonomic species (*C. arcticum* s.s. and *C. nigrescens* (H. C. Watson) Edmondston ex H. C. Watson; Brysting & Borgen, 2000; Brysting & Elven,

2000; Hagen, Giese & Brochmann, 2001). Both lineages are amphi-Atlantic, and evidence from RAPD and SCAR analyses suggests that they both have dispersed recently (probably post-glacially) across the Atlantic although they lack mechanisms promoting long-distance dispersal. This finding agrees with many other recent studies suggesting that arctic species can disperse over much longer distances in much shorter time than traditionally assumed (reviewed in Abbott & Brochmann, 2003; Brochmann *et al.*, 2003).

Phylogenetic relationships and biogeography of 57 taxa representing the entire genus were studied using sequences of three non-coding plastid DNA regions (*trnL* intron, *trnL-trnF* spacer and *psbA-trnH* spacer) by Scheen *et al.* (2003, 2004). Five major clades were identified, suggesting an origin in Central Asia and at least two migration events from this region into North America. The oldest migration event involved low ploids and possibly took place across the Bering land bridge during the Miocene, resulting in subsequent colonization of South America. A much more recent migration event into North America took place during the Quaternary, resulting in the current circumpolar distribution of the arctic species. The arctic species, which are octo- to dodecaploid, formed an unresolved monophyletic group together with some boreal high-level polyploids. This arctic-boreal clade probably diverged 0.4–1.6 Mya, perhaps coinciding with the onset of the major Pleistocene glaciations. Most of the arctic species have identical cpDNA sequences, and they occur over vast and partly different geographical areas (e.g. amphi-Pacific, amphi-Atlantic and circum-arctic). This pattern suggests recent origins, rapid dispersal over vast distances, and recurrent episodes of range expansions and contractions during the Quaternary glaciations.

OTHER EXAMPLES OF COMPLEX RETICULATIONS

Evidence for complex and recurring reticulations has also been presented for several other arctic-alpine plant groups. In *Saxifraga*, two narrow Scandinavian endemics (*S. svalbardensis* Øvstedal in Svalbard and *S. opdalensis* A. Blytt in southern Norway) have probably originated *in situ* after the last glaciation, but in contrast to *S. osloensis* discussed above, they merely represent the current reticulate endpoints of a far more complex history of reticulate evolution (Brochmann *et al.*, 1998; Steen *et al.*, 2000). Evidence from a variety of molecular markers suggests that these two endemics have originated independently via post-glacial hybridization between the same two widespread species, the octoploid *S. rivularis* L. and the variable polyploid *S. cernua* L. Although the same parental species were involved, in both cases with *S. rivularis* as the maternal parent and *S. cernua*

as the paternal parent, *S. svalbardensis* and *S. opdalensis* are morphologically distinct and are commonly recognized as different taxonomic species.

The parental species of these endemics, *S. rivularis* and *S. cernua*, are themselves allopolyploids, and thus of hybrid origin, as evidenced by their fixed heterozygosity at isozyme loci. Molecular data suggest that one of the progenitors of the octoploid *S. rivularis* was *S. hyperborea* R. Br., a widespread arctic tetraploid (Brochmann *et al.*, 1998, and M. Jørgensen, T. M. Gabrielsen, R. Elven & C. Brochmann, unpubl. data). The situation in *S. cernua* is more complex. This species comprises a range of lineages with different chromosome numbers, some of them even co-occurring at small spatial scales, of which the low-ploid ones may have given and still continue to give rise to the high-ploid ones. Recent AFLP data suggest that one of the diploid progenitors of *S. cernua* is *S. sibirica* L. (M. Kapralov, T. M. Gabrielsen & C. Brochmann, unpubl. data). Thus, the current, post-Weichselian endemics *S. svalbardensis* and *S. opdalensis* have ultimately combined a number of ancestral diploid genomes with different evolutionary histories, inherited via repeated reticulations that have occurred throughout the complex Quaternary history of the arctic flora.

Poa evidently has a similar history of complicated reticulations at different scales in time and space. This genus contains many arctic taxa with high and variable chromosome numbers. There is now strong molecular and GISH evidence for recent recurrent origins of the North Atlantic endemic *Poa jemtlandica* (Almq.) K. Richt., via hybridization between two widespread polyploids that have a longer history of reticulate evolution (*P. alpina* L. and *P. flexuosa* Sm.; Brysting, Elven & Nordal, 1997; Brysting, Holst-Jensen & Leitch, 2000).

In *Draba* (Brassicaceae), there are some arctic diploids and numerous arctic allopolyploids, up to 18-ploid. In this genus, molecular data combined with evidence from morphology and crossing relationships indicate extremely complex evolutionary patterns, ranging from recent, independent and local formation of similar polyploids to multiple origins of widespread, high-polyploid taxa (Brochmann, Soltis & Soltis, 1992a,b,c; summarized in Brochmann, 1992).

The high ploidal levels, complex evolutionary history and wide geographical distribution of many arctic plant groups necessitate detailed and comprehensive approaches to the study of polyploid origins. It is difficult to delimit appropriate study groups based on morphology, because all diploid progenitors may not necessarily express their morphological fingerprints in a polyploid derivative. *Silene* (Caryophyllaceae) provides an excellent illustration of this situation (Popp, Erixon & Oxelman, 2003). Based on seven DNA regions, including sequencing of paralogues of nuclear

low copy genes, it was unambiguously demonstrated that the diploid progenitor lineages of a circumpolar complex of arctic tetra- and hexaploid species (*S. involucrata* Cham. & Schlecht., *S. ostenfeldii* (Porsild) Petrovsky & Elven comb. nov. prop., and *S. sorensenii* (Boivin) Bocquet) were represented by the *S. uralensis* (Rupr.) Bocquet and the *S. linnaeana* V. N. Vorosch. (*Lychnis sibirica* L.) groups. Whereas *S. uralensis* is morphologically similar to the tetra- and hexaploids, the *S. linnaeana* group is morphologically quite different and has never been suggested to be closely related to these arctic polyploids. Notably, *S. linnaeana* has usually been assigned to another genus, *Lychnis* L., and most recently to the genus *Sofianthe* Tzvelev (Tzvelev, 2002).

GENETIC AND ECOLOGICAL CONSEQUENCES OF ARCTIC POLYPLOIDY: SVALBARD AS A MODEL AREA

The high arctic, isolated Atlantic archipelago of Svalbard ('Spitsbergen'; 77–81°N; Fig. 2) was almost completely glaciated during the maximum of the last glaciation (Landvik *et al.*, 1998, 2003). Most, if not all, of the present species must therefore have immigrated postglacially, i.e. during the last 10 000–15 000 years. The molecular data obtained for plant and animal populations in Svalbard so far reveal very close relationships to conspecific populations to the west (Greenland), east (Russia) and/or to the south (Scandinavia), suggesting recent immigration from these areas (reviewed in Brochmann *et al.*, 2003).

Today, the Svalbard flora is probably the best known

among all arctic floras with respect to molecular diversity (isozymes and/or DNA data available for some 70 of the 161 native species and subspecies), chromosome numbers (available for 97.5% of the species, more than half of them counted on Svalbard material) and reproductive biology. Thus, the archipelago can serve as a model area for the study of arctic polyploidy and effects of immigration after recent deglaciation. A detailed analysis of the available data was provided by Brochmann & Steen (1999). Herein we summarize the main results of that study as well as report new data. In particular, many more species have now been examined for variation and duplications at isozyme loci.

Most (78.3%) of the 161 native taxa are polyploid. The average ploidal level based on all species, including diploids, is close to hexaploid (5.4), and many species have very high ploidal levels. All of the 47 polyploids examined for variation at isozyme loci are fixed heterozygotes, i.e. they are genetically allopolyploid with disomic inheritance (Fig. 5). Fixed heterozygosity has been inferred from absence of segregation in progeny tests of many of the species; for other species it has been inferred from fixed variation among individual plants in natural populations. Occasional segregation at a few loci has been observed in a few plants only.

Most of the few extant diploid species in Svalbard are highly homozygous because of regular self-fertilization. The level of heterozygosity in the polyploids can be expressed as the number of different homomeric and monomeric enzyme bands they express at their duplicated loci, which can be termed 'allo-alleles' as opposed to normally segregating alleles

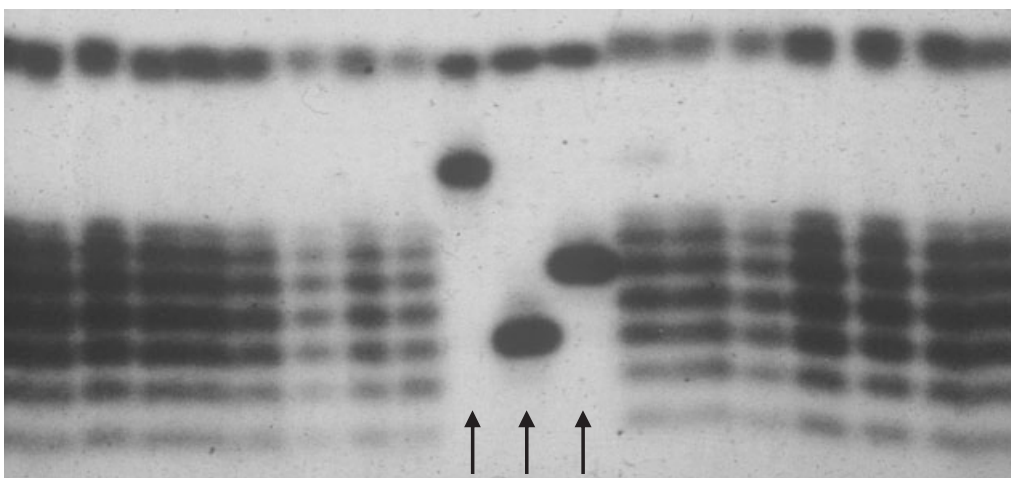


Figure 5. Variation at the duplicated cytosolic GPI (glucose-6-phosphate isomerase) locus in a typical Svalbard polyploid, which is highly fixed-heterozygous and clonal or self-pollinating with low levels of intrapopulational variation. Exemplified by the decaploid and highly selfing *Draba alpina*, and, designated by arrows, three homozygous marker plants of the highly selfing diploids *D. fladnizensis*, *D. nivalis* and *D. subcapitata* Simmons (Brochmann *et al.*, 1992a).

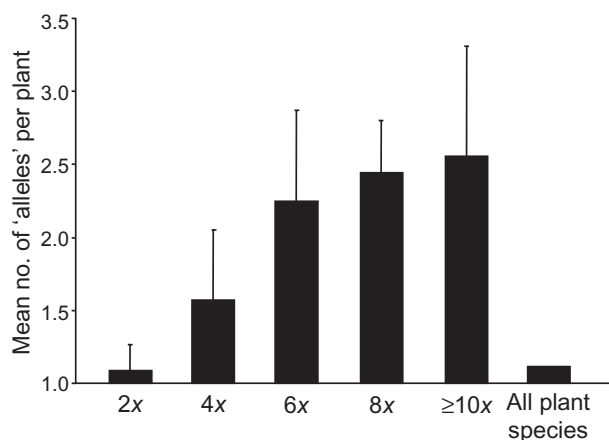


Figure 6. Levels of 'heterozygosity' observed for cytosolic GPI (glucose-6-phosphate isomerase) in 65 species (363 populations, 3509 plants) with different ploidal levels from the isolated North Atlantic archipelago of Svalbard. Calculated as mean number of different alleles per plant in the diploids and as mean number of different 'allo-alleles' at duplicated loci per plant in the polyploids, which exclusively show fixed heterozygosity. Standard deviations are indicated by lines. The investigated species represent 40% of the entire Svalbard flora. The mean value for 'all plant species' is given for comparison, based on isozyme data compiled by Hamrick & Godt (1989). For Svalbard, the data are based on 18 diploids (103 populations, 1376 plants), 18 tetraploids (110 populations, 961 plants), eight hexaploids (54 populations, 388 plants), ten octoploids (44 populations, 402 plants), eight polyploids at or above the decaploid level (39 populations, 272 plants) and three polyploids with unknown ploidal level (C. Brochmann, S. Spjelkavik, J. Haugen & N. W. Steen, unpubl. data).

at a single locus. The level of heterozygosity increases strongly with ploidal level. In Figure 6, this is illustrated by the mean number of different alleles in the diploids and allo-alleles in the polyploids observed per plant for cytosolic GPI (glucose-6-phosphate isomerase) in 363 Svalbard populations of 65 species (C. Brochmann, S. Spjelkavik, J. Haugen & N. W. Steen, unpubl. data). The maximum number of different allo-alleles observed in a single plant at this locus is six (the 16-ploid *Draba corymbosa* R. Br.). The total 'biochemical diversity' in this plant, i.e. including all different variants (homomers and heteromers) of the GPI enzyme produced in its cells, is 21, as compared with one in a homozygous diploid. Thus, this and many other Svalbard plants are not only heterozygous and biochemically diverse, but highly so. Although the post-Weichselian flora of Svalbard has low species richness in terms of taxonomic species, these species represent considerable genetic diversity, originally inherited from a much larger stock of diploid ancestral species.

It is probable that the genetic variation stored as fixed heterozygosity within individual plants sometimes can be released via occasional pairing of homoeologous chromosomes and translocation events. Data that may suggest interlocus recombination have been obtained from Svalbard populations of the hexaploid *Draba lactea* Adams. At the cytosolic GPI locus, most populations of this species were dominated by a five-banded phenotype (produced by three different allo-alleles), but a three-banded phenotype occurred at low frequencies in several geographically distant populations (Scheen, Elven & Brochmann, 2002). Although the five-banded phenotype previously had been shown to be fixed among large progeny arrays obtained after selfing (Brochmann *et al.*, 1992a), the three-banded phenotypes may have originated independently in different populations after similar translocation events, which broke up the normally fixed-heterozygous five-banded patterns.

All Svalbard taxa examined so far are self-compatible. Self-pollination efficiency has been tested in 53 taxa, 18 of them in Svalbard, and it is estimated that 75% of the species mainly, but not exclusively, reproduce by self-pollination. Nearly half of the species reproduce asexually, at least to some extent. Some species appear to reproduce entirely asexually. However, in one such species, the bulbil-reproducing *Saxifraga cernua*, clonal (RAPD) diversity is very high even at small spatial scales, suggesting that sexual events are more frequent than estimated from the rarity of seed set observations (Gabrielsen & Brochmann, 1998).

In many other taxa, however, there is little variation at AFLP, RAPD and isozyme loci among plants within populations because of predominant self-pollination or asexual reproduction. In some taxa, different Svalbard populations are genetically divergent, whereas other taxa comprise populations that all may contain a single, identical genotype. The level of variation among populations in Svalbard is probably highly dependent on the particular post-Weichselian colonization history of each taxon, in particular the number of independent long-distance dispersal events. Several species have probably immigrated several times. Most of the taxa occurring in Svalbard today are evidently good long-distance dispersers and successful colonizers, as inferred from their very wide geographical distributions. The majority (71%) of the taxa have complete circumpolar distributions and 22% of them are amphiatlantic. Only three taxa (2%) are currently recognized as endemic to this archipelago. One of these endemics has originated via post-Weichselian hybridization (*Saxifraga svalbardensis*; Brochmann *et al.*, 1998), and the two others (*Potentilla insularis* Soják and *Puccinellia svalbardensis* Rønning) are only marginally different from Greenlandic and Russian plants.

Populations of outcrossing diploids typically become genetically depauperate when exposed to inbreeding and bottlenecks, for example in connection with long-distance colonization. By contrast, individual populations of the typical arctic plant, which is allopolyploid, may maintain most of their genetic variation in spite of inbreeding and bottlenecks, because each plant individual carries most of the population's gene pool in the form of fixed heterozygosity. Packing of ancestral genes into highly fixed-heterozygous, duplicated genomes ensures that genetic diversity is maintained through periods of extreme inbreeding and bottlenecks, for example when a deglaciated area is re-colonized by a single long-distance dispersed seed.

The optimal conservation strategy for most of the taxa (estimated to 93%) in Svalbard, and generally in the Arctic, is therefore to conserve many, small and spatially separated populations rather than few and large populations. Only nine Svalbard species, among them *Silene acaulis* (L.) Jacq., are outcrossing diploids with a considerable proportion of their genetic variation stored within populations. The remaining 19 diploid taxa occurring in Svalbard are predominantly selfing, highly homozygous and usually with very little intrapopulation variation. In the polyploids, most of the genetic variation is found as fixed heterozygosity and as variation among different populations.

High levels of heterozygosity have been suggested as a driving force for polyploids to expand into habitats beyond the limits of their progenitors (reviewed by Levin, 2002). The possibility for a connection between the evolutionary success of arctic polyploids, increased heterozygosity and ecological amplitude was explored in the genus *Draba*, which contains some arctic diploids and numerous polyploids (Brochmann & Elven, 1992). The occurrence of 443 populations of 16 diploid and polyploid species ($4x$ – $16x$) in different habitat types in Svalbard and Scandinavia was recorded, and the amplitude of each species was expressed by Shannon–Weaver indices. The ecological amplitude of the species as well as their levels of heterozygosity and biochemical diversity increased significantly with ploidal level.

In *Draba*, these results as well as evidence for multiple origins of polyploids and gene flow across different ploidal levels through semifertile hybrids led to the hypothesis that allopolyploidy may serve as an escape from genetic and ecological depauperation caused by drift and uniparental inbreeding at the diploid level (Brochmann, Stedje & Borgen, 1992d; Brochmann, 1992, 1993). In the diploids, regular inbreeding by self-pollination ensures sexual reproduction in the severe arctic environment where pollinating insects are scarce, but inevitably results in genetic and ecological depauperation.

SIBLING SPECIES IN ARCTIC DIPLOIDS – NEW RAW MATERIALS FOR POLYPLOID FORMATION?

The contemporary arctic flora, even when including the boreal borderline taxa (Table 1), certainly contains too few diploid taxonomic species to explain the high number of high-level allopolyploid taxa. It has been suggested that many of the diploid progenitors of the current arctic allopolyploids went extinct during the dramatic climate changes, which the polyploids were better able to survive, and/or that many of them were left behind when their polyploid derivatives dispersed from their alpine source areas into the Arctic (see, for example, Stebbins, 1984, 1985).

However, recent experimental data suggest that the diversity at the diploid level in the contemporary arctic flora is higher than estimated from the number of taxonomic species. In the strongly autogamous diploid *Draba fladnizensis* Wulfen, crossing experiments revealed that it consists of at least two biological (sibling) species in the North Atlantic (Brochmann, Borgen & Stedje, 1993). Crosses between morphologically indistinguishable populations of this species from Scandinavia and Svalbard resulted in F_1 hybrids that were vigorous and luxuriantly flowering, but entirely sterile. However, the meiosis was regular, indicating that their sterility was caused by minor mutations.

Further crossing experiments at the circumpolar scale within this taxonomic species and within another autogamous diploid, *Draba nivalis* Lilj., have revealed numerous incompatible combinations (Grundt *et al.*, 2001; Grundt, 2003). Thus, these two easily recognizable and apparently good taxonomic species must represent numerous sibling or cryptic species in the circumpolar Arctic. Phylogenetic and geographical relationships among populations within each of these two taxonomic species, inferred from AFLP markers, show little congruence with their crossing relationships. This result suggests that crossing barriers arise rapidly and are based on a single or few mutations only.

It is possible that formation of crossing barriers is a rapid and common process in small and fragmented populations of highly selfing diploids in the Arctic, promoting divergent evolution also within currently recognized taxonomic species. Evolution of crossing barriers inhibits mixing of populations that have diverged in different glacial refugia and later re-immigrated to the same deglaciated area.

Allotetraploids are thought to originate normally via hybridization between two cross-incompatible, divergent diploid species that will produce sterile hybrids if chromosome doubling does not occur. It is tempting to suggest that also sibling diploid species occasionally can hybridize and form genetically allopolyploid, but

taxonomically autopolyploid, derivatives, thus adding yet another level of complexity to arctic plant evolution. The hexaploid *Draba lactea* has, for example, been suggested to be an auto-allopolyploid composed of two diploid genomes from *D. fladnizensis* and one diploid genome from *D. nivalis* (Böcher, 1966). However, as outlined above, this hexaploid is completely fixed-heterozygous at isozyme loci, suggesting that it is composed of three homoeologous diploid genomes (Brochmann *et al.*, 1993; Scheen *et al.*, 2002). If these genomes were contributed by sibling diploid species, *D. lactea* would genetically represent an allohexaploid but taxonomically an autohexaploid. Recent phylogenetic analysis of this hexaploid based on sequencing of cloned copies of ITS and nuclear low copy genes has suggested that it may have originated from a single diploid lineage (Grundt, 2003).

The large variation observed in number of different 'allo-alleles' at isozyme loci among different arctic polyploids at the same ploidal levels (Fig. 6) may indeed reflect that some polyploids were formed from highly divergent diploids and others from diploids that were much more closely related, although all of these polyploids are genetically allopolyploid. The more divergent the diploid progenitors were, the more likely it is that they contributed with different alleles at a particular locus. In the *Dupontia* case outlined above, the highest polyploids are apparently fixed-heterozygous but nevertheless contain similar numbers of different 'allo-alleles' as the hexaploids (A. K. Brysting, unpubl. data). This pattern suggests that whereas the hexaploid itself originated from divergent diploids, the higher polyploids were formed from hexaploid populations that were very closely related.

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